ESTIMATION OF GROWTH RATE IN ANIMALS BY MARKING EXPERIMENTS

By MILTON J. LINDNER, *Fishery Research Biologist*

Effective action to conserve an animal resource must be based on such vital statistics as age composition of the stock and rates of mortality, replacement, and growth. In some species of animals, but unfortunately not in all, age and growth are indicated by the occurrence and spacing of rings on such hard parts as scales, bones, and shells. In studying shrimp (*Penaeus setiferus*) along the southern coast of the United States I found the problem of age determination particularly difficult, since no skeletal structures are carried over from one molt to another. Researchers studying other Crustacea report the same difficulty, with the result that growth of such important species as lobsters and crabs is imperfectly known.

The method for estimating growth described here can be used wherever growth follows geometric progression. It can be used in laboratory feeding experiments and with animals of unknown ages, and it is particularly useful when the age of animals cannot be ascertained by any other means. Although I stress the growth aspect in this paper, it is obvious that the method can be used also for determining age (only within the limits for which the technique is valid for growth) simply by plotting the results in the usual manner with size against time.

For equal time intervals Walford (1946) has demonstrated for many animals that growth, above the point of inflection on the curve of absolute growth, may be plotted as a straight line. This is accomplished by plotting the length at ages 1, 2, 3, 4 . . . on the X axis against length at ages 2, 3, 4, 5 . . . $n+1$ on the Y axis. The slope of this line is k. On the line, the length relations are such that:

$$L_n=\frac{1-k^n}{1-k}, L_{n+1}=L_1\,\frac{1-k^{n+1}}{1-k}\,k, =1-\frac{L_1}{L_\infty},$$

$$\text{and } L_\infty=\frac{L_1}{1-k}.$$

L_∞ represents the ultimate length, which is also the point where this transformed growth line intersects the 45° line, or where $X=Y$.

Walford's transformation, which is based on the sizes of animals of known ages, can be modified to determine the growth rate of animals of unknown ages. This can be done because the time intervals are uniform or constant. As a consequence, if we take the lengths of a group of animals of unknown ages and of varying sizes on a certain day and measure these same animals again 1 year later, we shall have their respective lengths at age n and at age $n+1$ year. Plotting lengths n against $n+1$ will result in Walford's transformation for one time interval, in this instance, 1 year. If we should measure these same animals 2 years later and plot them in the same fashion (n against $n+2$), we should have a growth line representing the increment for 2-year intervals. From the relations between these lines we can arrive at the growth rate of an animal for any time interval we choose. The time interval, of course, must be constant.

A graphical representation of the relation between transformation lines obtained by plotting n against $n+1$, $n+2$, $n+3$, and so on, is shown in figure 1. Line A represents the transformed growth for one time interval, or Walford's transformation (n against $n+1$), line B for two time intervals (n against $n+2$), line C for three intervals (n against $n+3$) and so on.

In each instance, the length of the horizontal lines extended from L_2 to intersect line A, from L_3 to line B, from L_4 to line C, and so on, are equal. The length of each line is also equal to L_1. Consequently, if we know the sizes of a number of animals of different ages on a certain date and can measure these same animals (or representative samples of them) at successively equal later intervals of time, we can determine their growth line (Walford line) for the time interval chosen. An

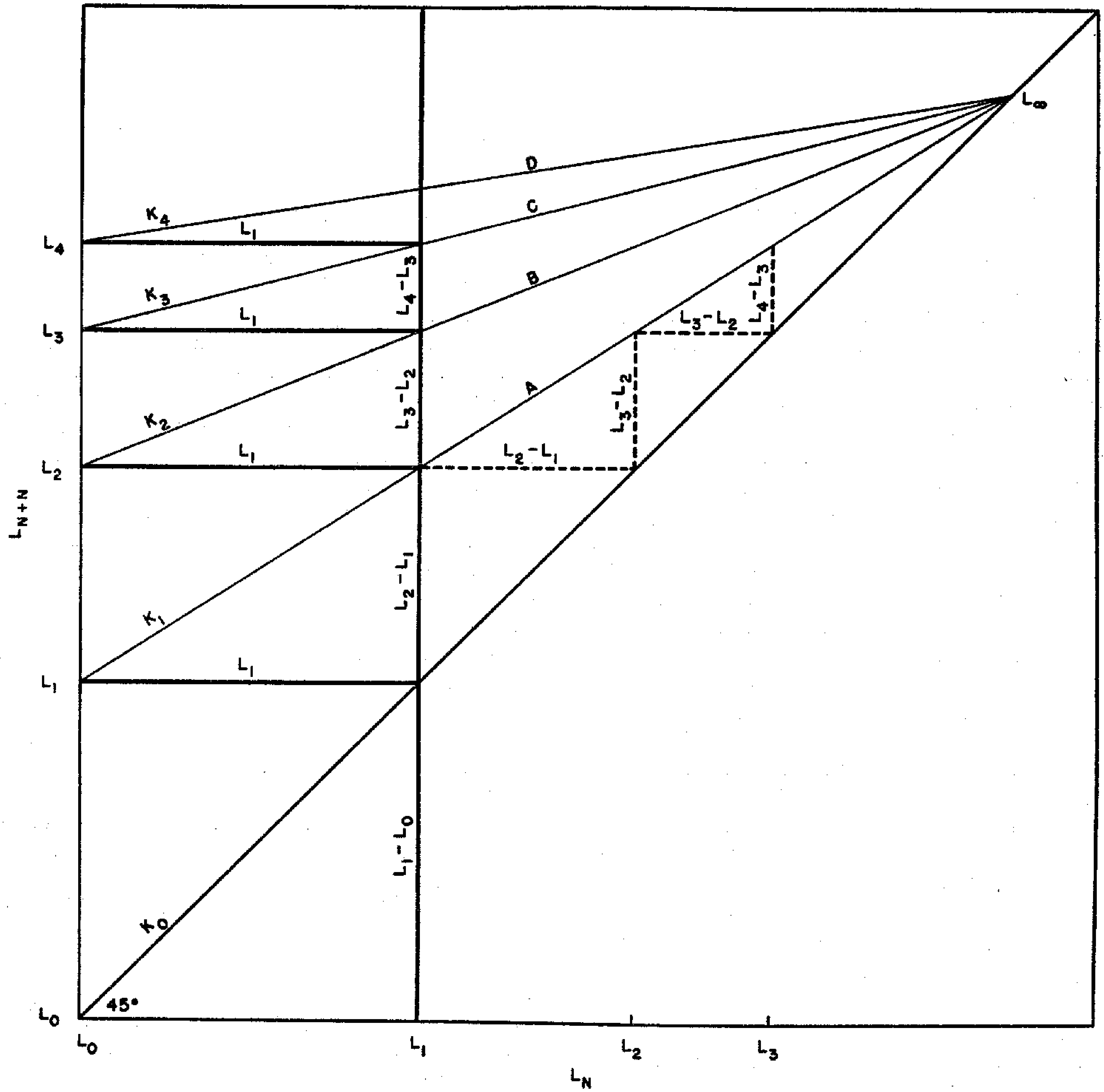

FIGURE 1.—*Relation between growth lines.*

estimate of L_1 can be obtained as just described, an estimate of L_∞ can be obtained from where the various lines intersect the 45° line drawn from zero, and k can be calculated from L_1 and L_∞.

The technique described is graphic. The same results can be obtained mathematically. The slopes of the various lines in figure 1 are

$$k_0=\frac{L_1-L_0}{L_1},\ k_1=\frac{L_2-L_1}{L_1},\ k_2=\frac{L_3-L_2}{L_1},$$

$$k_3=\frac{L_4-L_3}{L_1},\ k_4=\frac{L_5-L_4}{L_1},\ \ldots\ k_n=\frac{L_{n+1}-L_n}{L_1}.$$

Consequently $L_1=\dfrac{L_{n+1}-L_n}{k_n}$ . . . . (1)

But $L_n=L_1\dfrac{1-k^n}{1-k}$ and $L_{n+1}=L_1\dfrac{1-k^{n+1}}{1-k}$.

Subtracting L_n from L_{n+1} we obtain

$$L_1k^n(1-k)=(1-k)(L_{n+1}-L_n)$$

or $L_1=\dfrac{L_{n+1}-L_n}{k^n}$ . . . . (2)

But $L_1=\dfrac{L_{n+1}-L_n}{k_n}=\dfrac{L_{n+1}-L_n}{k^n}$; consequently $k_n=k^n$.

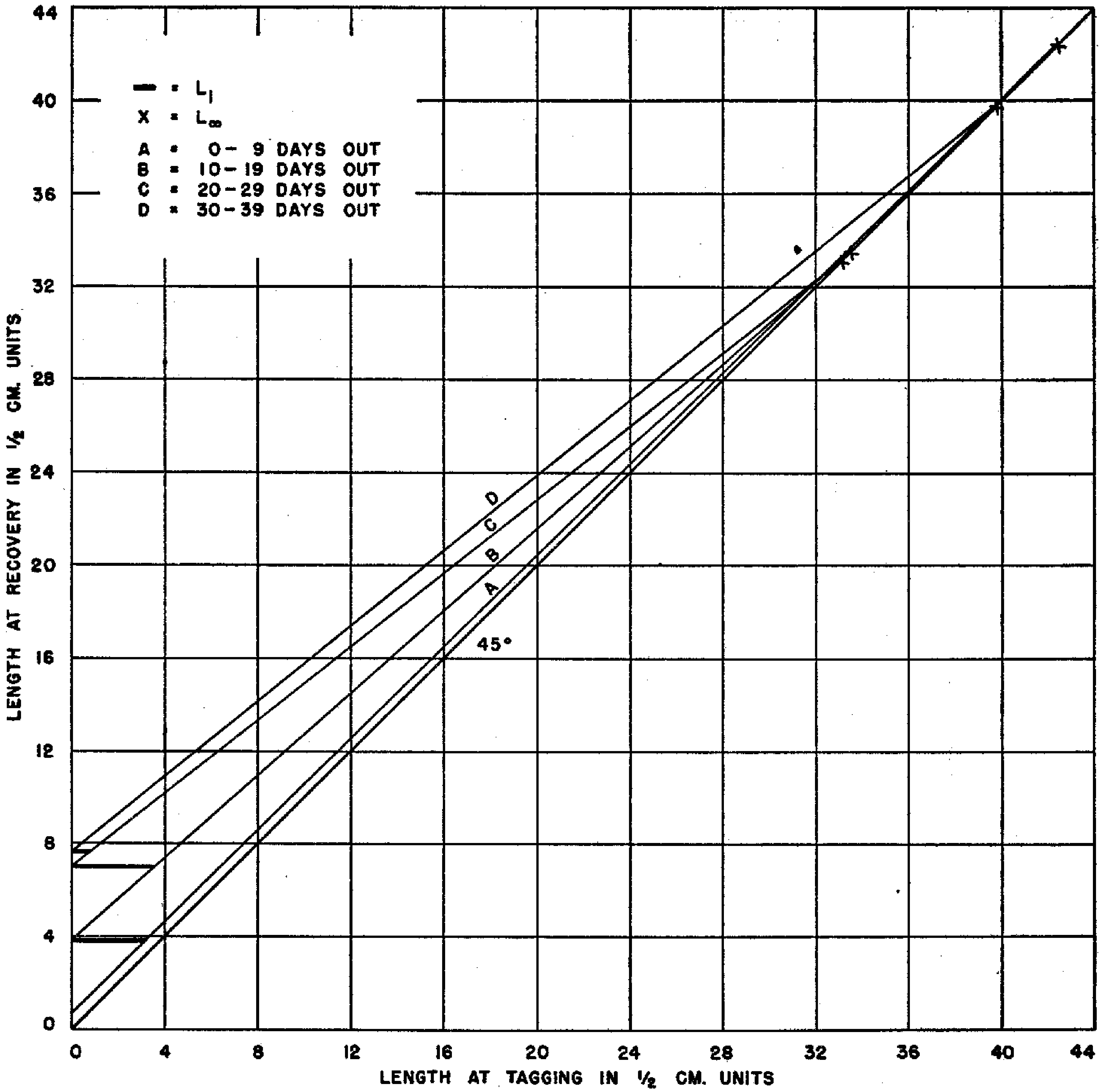

FIGURE 2.—Growth lines determined from marked shrimp, with estimates of L_1 and L_∞.

In Walford's transformation the two important points are L_∞ and L_1. These are obtained where $Y=X$ and where $X=0$, respectively.

L_∞ can be calculated readily from the fact that $Y=a+bX$ and when $Y=X$, also $Y=\frac{a}{1-b}=L_\infty$. (3)

Where L_1 is being obtained from two or more transformation lines, approximations can be reached by using formula 1.

When transformation lines can be obtained from two or more successive time intervals, approximations to L_∞ and L_1 can be obtained from their respective means.

As an example of this procedure, I am giving here the processes followed in obtaining a growth approximation from an experiment with marked shrimp.

As Walford (1946) has cautioned, a great many specimens are required for an accurate approximation to a growth line. The experiment I cite has very few specimens and cannot be regarded as representing growth in shrimp (*Penaeus setiferus*). I use it only to demonstrate the technique. As a matter of fact, because of the variability of the data I believe that, in an example such as this, results just as significantly accurate could be obtained by merely plotting the data, fitting the lines by eye, and estimating the L_1's and L_∞'s from the graph.

Between September 20 and 25, 1939, we measured in ½-cm. units and marked a number of shrimp in the Gulf of Mexico. We measured the shrimp again upon recapture.

I divided the returns (sexes combined) into four equal time intervals of 10 days each—0 to 9 days out, 10 to 19 days out, 20 to 29 days out, and 30 to 39 days out—and arranged the number of returns in tabular form with lengths at tagging against lengths at return. I fitted lines by least squares to these data, with X=length at tagging and Y=length at return. See tabulation following and figure 2.

Number of days out	Number of shrimp marked	Line formula	L_∞	L_1
0–9	314	Y=0.678+0.984X	42.38	
10–19	72	Y=3.850+ .885X	33.48	3.22
20–29	30	Y=6.984+ .789X	33.10	3.54
30–39	35	Y=7.600+ .809X	39.79	0.78
Sum			106.37	7.54
Mean			35.46	2.51

In the tabulation, L_∞ for 0–9 days out was not used in calculating the sum or the mean L_∞ as it represents only an average of 5 days' growth. In using this technique I wish to caution against taking too short a time interval or too large a measuring unit. There is always the possibility under these circumstances that L_∞ will be either too large or too small. When the growth line tends to parallel the 45° line, L_∞ will be too large. When L_∞ tends to represent the larger individuals at time of marking, it generally will be too small. In this instance the tendency was to approximate the 45° line, probably making L_∞ too large.

In each instance, I calculated L_∞ from the constants in the line formula and from $L_\infty=\frac{a}{1-b}$.

For example, for 0–9 days out $L_\infty=\frac{0.678}{1-0.984}=42.38$ ½-cm units or 211.9 mm.

I calculated L_1 from two successive lines and the formula $L_1=\frac{L_{n+1}-L_n}{k_n}$.

For example, L_1 calculated from the 0–9 and 10–19 day lines is $L_1=\frac{3.850-0.678}{0.984}=3.22$ ½-cm. units.

I obtained Walford's 10-day growth line from the mean L_∞ and the mean L_1 and from the formula $k=1-\frac{L_1}{L_\infty}$; $k=1-\frac{2.51}{35.46}=0.9292$.

Hence, Walford's line for 10-day intervals for this group of shrimp is Y=2.51+0.9292X.

However, in order to compare growth calculated in this fashion with monthly size distributions of the shrimp populations, I found it necessary to have a 30-day instead of a 10-day Walford line. In other words, I needed an L_3 instead of an L_1 line. This was obtained by

$$L_3=L_1\,\frac{1-k^3}{1-k}=2.51\,\frac{(1-0.9292^3)}{1-0.9292}=7.01;$$

$$k_3=1-\frac{L_3}{L_\infty}=1-\frac{7.01}{35.46}=0.8023.$$

Hence, for a 30-day Walford line in ½-cm units Y=7.01+0.8023X.

LITERATURE CITED

Walford, Lionel A.
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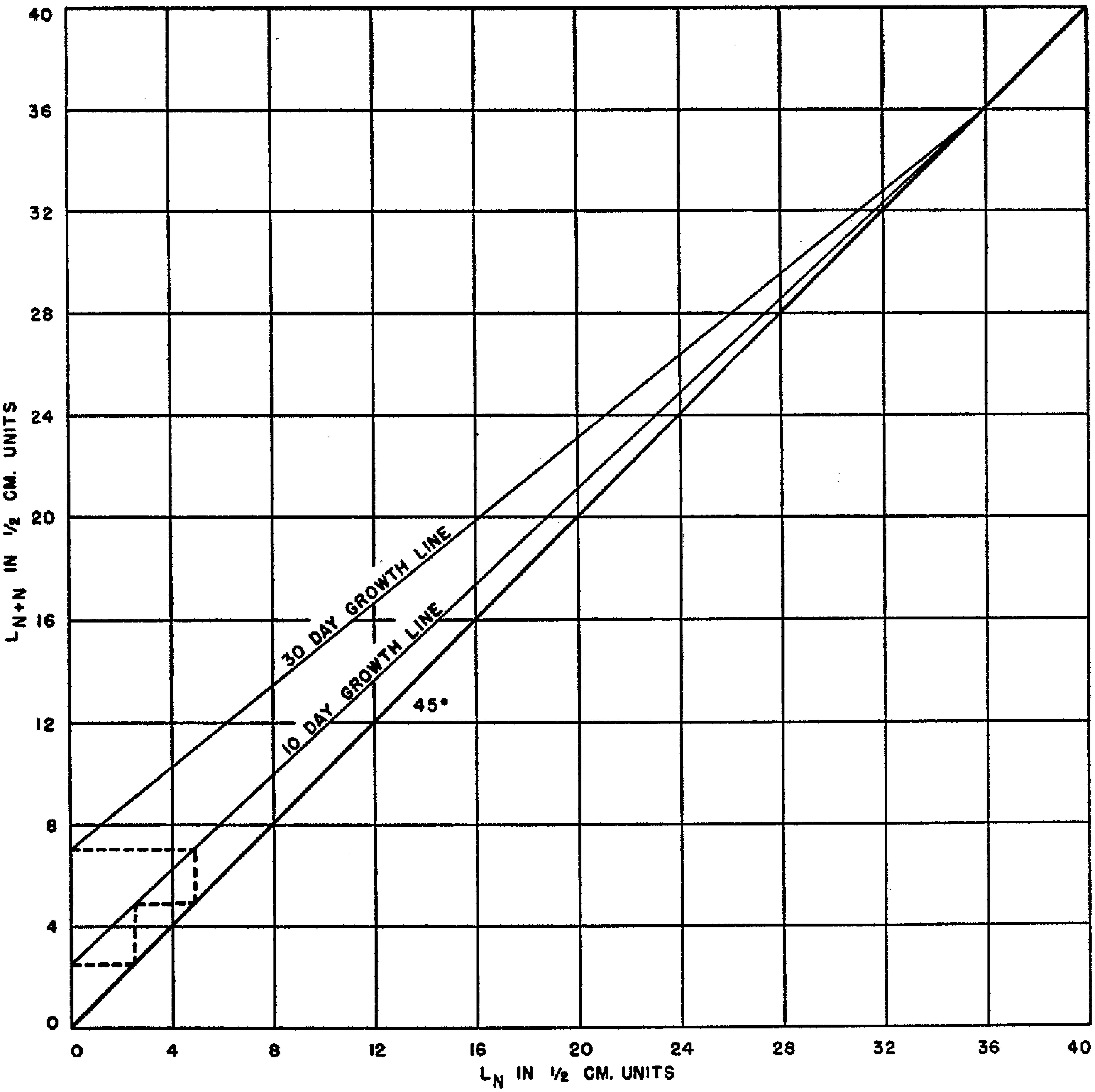

FIGURE 3.—Ten-day and thirty-day growth lines determined from mean estimates of L_1 and L_∞.